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Contrasting effects of large herbivore grazing on smaller herbivores

E.S. Bakker[a,*], H. Olff[b,c], J.M. Gleichman[a]

[a]*Nature Conservation & Plant Ecology Group, Wageningen University, Bornsesteeg 69, 6708 PD Wageningen, The Netherlands*
[b]*Resource Ecology Group, Wageningen University, Bornsesteeg 69, 6708 PD Wageningen, The Netherlands*
[c]*Community and Conservation Ecology Group, Centre for Evolutionary and Ecological Studies, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands*

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Abstract

Assemblages of large herbivores may compete for food or facilitate one another. However, small vertebrate herbivore species co-occurring with large herbivores may be affected by large herbivore grazing through changes in plant species composition, nutrient content and vegetation structure. These changes can be either positive or negative for the smaller herbivores, but this may depend on the species of small herbivores. We experimentally tested the impact of cattle grazing on habitat choice of European rabbits (*Oryctolagus cuniculus*) and common voles (*Microtus arvalis*). We excluded cattle for 7 years and measured changes in vegetation parameters, and the response of rabbits and voles. Rabbits were facilitated by cattle, whereas voles strongly preferred vegetation without cattle. The facilitation effect was stronger at low rabbit densities. Vegetation biomass and nitrogen concentration were not affected by cattle grazing, but vegetation height increased significantly where cattle were excluded. Plant species composition also changed following cattle exclusion; however, the main food plants of rabbits and voles remained abundant in each grazing treatment. We conclude that the response of both rabbits and voles predominantly reflect the differences in vegetation height in the presence and absence of cattle, but in a contrasting fashion. The difference in response between rabbits and voles may result from reduced perceived predation risk, which is lowest in high vegetation for voles, but in short vegetation for rabbits, which depend on their burrows for safety. The use of large herbivores in grassland conservation management can thus have a contrasting effect on different species of small herbivores.

Zusammenfassung

In Vergesellschaftungen können große Herbivore um Nahrung konkurrieren oder sich gegenseitig fördern. Kleine herbivore Wirbeltierarten, die zusammen mit den großen Herbivoren vorkommen, können durch die Beweidung durch die Herbivoren beeinflusst werden, indem die Pflanzenartenzusammensetzung, der Nährstoffgehalt oder die Vegetationsstruktur verändert wird. Diese Effekte können sich entweder positiv oder negativ für die kleineren Herbivoren auswirken und das könnte von der Art der kleineren Herbivoren abhängen. Wir untersuchten experimentell die Auswirkungen der Rinderbeweidung auf die Habitatwahl von europäischen Kaninchen (*Oryctolagus cuniculus*) und Feldmäusen (*Microtus arvalis*). Wir schlossen die Rinder für 7 Jahre aus und bestimmten die

*Corresponding author at: Department of Plant–Animal Interactions, Netherlands Institute of Ecology (NIOO-KNAW), Rijksstraatweg 6, 3631 AC Nieuwersluis, The Netherlands. Tel.: +31 294 239357; fax: +31 294 232224.
E-mail address: l.bakker@nioo.knaw.nl (E.S. Bakker).

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Veränderungen der Vegetationsparameter und die Reaktionen der Kaninchen und Feldmäuse. Die Kaninchen wurden durch die Rinderbeweidung gefördert, während die Feldmäuse die Vegetation ohne Beweidung stark bevorzugten. Der Förderungseffekt war bei geringeren Kaninchendichten stärker. Die Biomasse der Vegetation und die Stickstoffkonzentration wurde durch die Rinderbeweidung nicht verändert, aber die Vegetationshöhe nahm bei Ausschluss der Rinder signifikant zu. Die Zusammensetzung der Pflanzenarten veränderte sich ebenfalls infolge des Rinderausschlusses. Die hauptsächlichen Futterpflanzen der Kaninchen und Feldmäuse blieben jedoch bei beiden Beweidungsvarianten häufig. Wir schließen daraus, dass die Reaktionen sowohl der Kaninchen als auch der Feldmäuse vor allem die Unterschiede in der Vegetationshöhe bei Anwesenheit oder Abwesenheit von Rindern widerspiegeln, jedoch in unterschiedlicher Weise. Die Unterschiede in den Reaktionen von Kaninchen und Feldmäusen können eine Folge des unterschiedlichen Prädationsrisikos sein, das für Feldmäuse in hoher Vegetation, für Kaninchen jedoch in kurzer Vegetation am geringsten ist, da sie sich auf die Sicherheit ihrer Bauten verlassen. Die Verwendung großer Herbivorer beim Grünlandmanagement zu Naturschutzzwecken kann deshalb gegensätzliche Auswirkungen auf verschiedene Arten der kleinen Herbivoren haben.

Keywords: Facilitation; Food; Grassland; Lagomorph; *Microtus arvalis*; Nitrogen; *Oryctolagus cuniculus*; Predation risk; Rabbit

Introduction

Grassland herbivores may compete for food or facilitate one another (Arsenault & Owen-Smith, 2002). Whether herbivores compete or facilitate has been found to depend on their difference in body size (Prins & Olff, 1998), but also on feeding style (grazers/browsers), digestive system and morphology (Bell, 1971; Du Toit & Owen-Smith, 1988; Hofmann, 1989). These herbivore traits have been successfully used to explain interactions within large herbivore assemblages (Olff, Ritchie, & Prins, 2002; Wilmshurst, Fryxell, & Bergman, 2000). However, many smaller-sized vertebrate grazers occur in grasslands, which may also interact with larger herbivores. Body size ratio rules predict that smaller herbivores do not compete with large ones since they can occupy different niches, due to different requirements of food quantity and quality (Belovsky, 1997; Demment & Van Soest, 1985; Illius & Gordon, 1992). However, the impact of an assemblage of large savanna herbivores has been shown to affect the occurrence of herbivorous rodents negatively, presumably due to competitive interactions (Keesing, 2000). Large mammalian herbivores can strongly affect grassland plant diversity (Olff & Ritchie, 1998) and functioning (Milchunas & Lauenroth, 1993) and subsequently change food availability for small herbivores. A shift in the vegetation community composition due to large herbivore grazing can result in a change in abundance of preferred plant species for small herbivores (Huisman & Olff, 1998). The diet choice of the small herbivore may affect its response to ungulate grazing. For example, in mountain grassland sheep grazing had differential effects on two herbivorous rodent species depending on their diet preferences (Steen, Mysterud, & Austrheim, 2005).

Grazing can also stimulate fresh re-growth of plants which is usually of better quality than mature leaves (McNaughton, 1984; Ydenberg & Prins, 1981). However, apart from changing food sources for small herbivores, grazing by large herbivores can also affect the degree of cover from predators (Schmidt, Olsen, Bildsoe, Sluydts, & Leirs, 2005; Smit et al., 2001). These factors do not necessarily change in the same direction – large herbivores may reduce food quantity and vegetation height or cover, but improve food quality for example. Hence, their effect on small herbivores is not immediately clear.

The importance of perceived predation risk for small herbivore habitat preferences may vary among herbivore species. Central-place foragers, such as prairie dogs and several rabbit species, use burrows as predator cover. Therefore, the fastest route to their burrow and a clear view may be more important than the cover in the immediate surrounding of their foraging station. Non-central-place foragers on the other hand, including many small rodent species, need shelter from aerial predators during foraging and are found to prefer tall vegetation (Jacob & Brown, 2000). Food availability may interact with the importance of predator cover. Small rodents are shown to take more risk for high quality food which is placed outside vegetation cover (Kotler & Blaustein, 1995).

Although the importance of these factors has been widely acknowledged, few studies which experimentally test the relationship between ungulate grazing and small mammalian herbivore abundance have measured the impact of ungulates on all relevant vegetation parameters. Information on small mammal diet is also frequently lacking.

In this study, we test whether large herbivore grazing affects vegetation structure, food quantity and food quality for smaller mammalian herbivores. We test whether different small herbivore species respond differently to large herbivore grazing, and whether these responses depend on diet preferences. We selected a

simple system to test this relationship using cattle and two distinctly different species of smaller mammalian herbivores co-occurring in a floodplain grassland: the European rabbit (*Oryctolagus cuniculus*) and the common vole (*Microtus arvalis*). We performed a field experiment where we excluded cattle and measured rabbit visitation rates to plots inside and outside the cattle fences over 7 years and vole abundances during the last 3 years of the experiment. We also determined rabbit and vole diets, as well as changes in vegetation community composition and vegetation height, together with changes in food quality and quantity following the exclusion of cattle.

Material and methods

Study site

The study was performed on Junner Koeland (52°32′N, 6°29′E), a 100-ha nature reserve including 50 ha of floodplain grassland along the river Overijsselse Vecht in the northeast of the Netherlands. The area was formerly common grazing land for the Junne village farmers, and has probably been grazed by livestock since the Middle Ages (Bokdam, 1987). Currently, cattle graze in the area from April to October with a density of 0.4 heifer ha^{-1}; the stocking rate since 1988. Naturally occurring grazers are rabbits and common voles. Dominant grasses in the floodplain meadows are the lawn-forming grasses *Festuca rubra*, *Agrostis capillaris* and to a lesser extent *Holcus lanatus* and *Luzula campestris*. Nomenclature follows Van der Meijden (1990).

Exclosure design

Five exclosures (blocks) were built in May 1994, evenly distributed over an area of approximately 1 ha. Each block consisted of three different 12×12 m grazing treatment plots (Fig. 1). Outside the fences, cattle, rabbits and common voles had free access to the vegetation. Barbed wire was used to exclude cattle but allow rabbits and voles to graze. Chicken mesh wire was used to exclude cattle plus rabbits, allowing only voles to graze the vegetation (Fig. 1).

Herbivore density

The cattle density was maintained over the years, at 0.4 heifers ha^{-1}.

We have previously shown that rabbit pellet density is strongly correlated with the number of grazed leaves per plot, as well as the number of observed rabbits at this site (Bakker, Reiffers, Olff, & Gleichman, 2005). Pellet

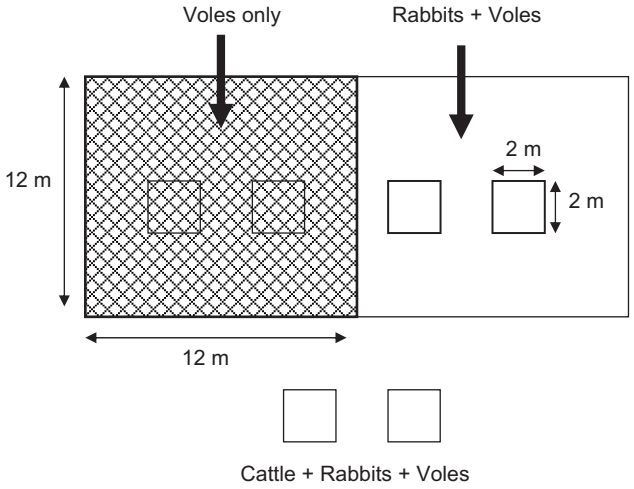

Fig. 1. Block design, indicating the three grazing treatments (Voles only, Rabbits + Voles and Cattle + Rabbits + Voles). Within each grazing treatment, two plots of 2×2 m were used to monitor vegetation composition, height and rabbit pellet density.

density was thus used as a measure of rabbit visitation to the grazing treatments. Each of the three grazing treatments contained two 2×2 m quadrats which were established following a randomized design, but were at least 1.5 m away from any fence (Fig. 1). Rabbit pellets were counted approximately every 3 weeks from 1994 until 2001 in all quadrats where rabbits had access, and pellets were removed after counting. Pellets found on latrines were excluded from the analysis of pellet rates because latrines have a social function, and pellets on latrines would not represent foraging activity. Rabbit visitation is expressed as pellet rate: the number of pellets m^{-2} day^{-1}.

Vole density was measured by live-trapping from 1998 to 2000. In 1998, three trapping sessions were established, in February, July and October, to determine seasonal peak vole density. In 1999 and 2000, trapping was conducted in October, during the peak vole density. Longworth live-traps, baited with peanut butter, oats, carrots and apple, and filled with some hay, were used throughout the study. Traps were pre-baited for 2 days before each 4-day trapping session, then checked every 8 h during each session, resulting in 11 checks per trap. In February 1998, trapping only lasted 3 days with a total of eight checks performed per trap. Captured voles were weighed, individually marked by clipping a piece of the fur at different positions on the back, and then released. Ninety traps were used per trapping session, six traps evenly distributed 3–4 m apart per grazing treatment, per block. In total 5040 trapnights were conducted. Since individual voles moved among grazing treatments, we could not use mark-recapture models to determine vole density per treatment and block.

Therefore, we compared two different measures of vole visitation – we assigned voles to the grazing treatment and block where they were first caught to obtain minimum numbers alive, and we calculated the total number of vole captures (including recaptures) in each grazing treatment and block. Vole trapping was approved by the committee for animal experiments (DEC) of Wageningen University.

Vegetation composition and height

Each year, from 1995 onwards, the vegetation composition was recorded during peak standing crop in late July or early August, following the decimal Londo scale (Londo, 1976). The vegetation composition was assessed in the same 2×2 m quadrats which were used to quantify rabbit density (Fig. 1). Since vegetation covered almost 100% of the soil surface in all quadrats, we used vegetation height as a measure of habitat structure. Vegetation height in the quadrats was measured following a grid system of 10×10 cells (each cell being 20×20 cm). Vegetation height was taken as the height at which a polystyreen disk (10-cm diameter) dropped from above rested on the vegetation (Stewart, Bourn, & Thomas, 2001). Vegetation height was measured during peak standing crop in 1994, 1995, 1997, 1998, 2000 and 2001 and in October 1998–2000.

Food quantity

Plant biomass was sampled in May, August and October 2001. Two random samples of 0.1 m^2 were clipped at soil surface in each grazing treatment plot outside of the 2×2 m plots. Locations were marked to avoid re-sampling of the vegetation. Biomass was separated into live and dead, with live material further separated into grasses and herbs. Biomass was dried for 48 h at 70 °C and weighed. Because voles and rabbits consumed a lot of seeds over the summer, flower (and seed) stem density was measured in June, July and October 2001. A circular frame of 0.5-m diameter was randomly thrown over the shoulder in a grazing treatment and the number of ungrazed flower stems within the frame was counted. Five frames were sampled within each grazing treatment plot.

Food quality

We determined nitrogen concentration in the plants as a measure of food quality. Because rabbit and vole diets consisted mostly of grasses, we measured nitrogen concentration of live grasses (mixed species) that were collected in May, August and October in the clipped plant biomass samples. Because a change in nitrogen concentration can be a direct effect of different grazing treatments or indirectly due to a shift in plant species composition, we separately measured the nitrogen concentration of green leaves of two dominant grass species (*H. lanatus* and *F. rubra*) in each grazing treatment. *Holcus* and *Festuca* were chosen because *Festuca* abundance decreased where cattle were excluded, whereas *Holcus* abundance increased. The dried grass samples were ground and digested with sulfuric acid, selenium and salicylic acid. The nitrogen concentrations were measured colorimetrically using a continuous flow analyzer (SKALAR San plus system; SKALAR, Breda, The Netherlands).

Herbivore diet

Diet of rabbits and voles was determined by analysis of epidermal fragments in droppings of both species (Cid & Brizuela, 1990; Sierra, Cid, Brizuela, & Ferri, 2005; Stewart, 1967), with leaves and fruits of 55 plant species from the study area as a reference collection. Droppings were collected monthly from May through December 2001. Fresh droppings were collected in our grazing treatment plots from at least three different blocks, with approximately 20 droppings collected per block. Droppings were pooled over blocks and grazing treatment plots to obtain one mixed sample per species per month. Samples were stored in the freezer until analysis. Epidermis fragments were identified and counted under the microscope using the line-transect method (Seber & Pemberton, 1979), with at least 100 fragments identified per sample. Fragments smaller than 0.01 mm^2 were generally ignored due to possible difficulties in identification. The surface of each fragment was measured to quantify its contribution to the herbivore diet. Measured fragment sizes and plant biomass consumed has been shown to be highly correlated for multiple species (Sierra et al., 2005). However, the methodology of microhistological analysis may lead to an underestimation of certain plant species which have a high digestibility (Cid & Brizuela, 1990; Vavra & Holechek, 1980).

Data analyses

When several samples had been collected within a single block and grazing treatment plot, these data were pooled before further analyses to avoid pseudoreplication, resulting in $n = 5$ in all analyses. Measurements taken repeatedly over time were analyzed with repeated measures ANOVA, followed by post-hoc Tukey tests. Data were log-transformed to obtain homogeneity of variances when necessary, as indicated in the text. For the vole capture data, homogeneity of variances could not be achieved due to a high number of zero values in the cattle-grazed treatment. Kruskal–Wallis tests were

used to analyze these data. We first tested whether there were significant differences among years and grazing treatments and, if so, subsequently tested differences among grazing treatments within years. We calculated average vole weight per grazing treatment assigning individuals to the plot on which they were captured the first time and pooled the weights of all individuals weighed within a block-treatment combination for each year. Average vole weight was calculated by averaging the weights among blocks, resulting in $n = 5$. We analyzed vole weights with a repeated measures ANOVA. Pearson correlation was used to examine the relationship between vegetation height in October, and October vole numbers and yearly rabbit pellet rates, by pooling the data from 1998, 1999 and 2000 and all grazing treatments where rabbits and voles had access to.

The cover of dominant plant species was compared among grazing treatments using Kruskall–Wallis tests for each species, as the variances were not homogeneously distributed even after transformation. Correspondence between the vegetation composition and rabbit and vole diet were tested using Pearson's correlation.

All analyses were conducted using Statistica 7.1 (StatsSoft Inc. 2005).

Results

Rabbit pellet rates

Rabbit pellet rates declined steeply during the course of the experiment (Fig. 2A, log-transformation: $F_{7,56} = 52.24$, $P < 0.001$). Overall, significantly more pellets were found in the presence of cattle (Fig. 2A, $F_{1,8} = 10.04$, $P = 0.01$). There was a significant interaction between year and grazing treatment ($F_{7,56} = 3.41$, $P = 0.004$); with a significant facilitation effect of cattle grazing during the second half of the experiment (Fig. 2A). This facilitation effect increased with the decrease in rabbit densities over time (Fig. 2B, $R^2 = 0.28$, $F_{1,38} = 14.57$, $P < 0.001$).

Vole numbers

Ninety-four percent of all animals caught ($n = 1877$) were common voles (*M. arvalis*), with common shrew (*Sorex araneus*, 4.7%), wood mouse (*Apodemus sylvaticus*, 1.2%) and watershrew (*Neomys fodiens*, 0.1%) making up the remaining 6%. Trap occupancy was 37%. Vole numbers were low in winter, then increased over summer, reaching peak densities in autumn (Fig. 3A). Vole numbers differed significantly among seasons and grazing treatments (Kruskal–Wallis test: $H = 36.75$, d.f. = 8, $P < 0.001$). The differences among grazing treatments became significant in July and October (Fig. 3A). The number of voles caught at peak vole density, in October, differed significantly among grazing treatments and years ($H = 30.55$, d.f. = 8, $P < 0.001$). Within each year, vole numbers were high in the absence of cattle, whereas in the presence of cattle, a few voles were caught in 1998, none in 1999 and one was recaptured in 2000 (Fig. 3B). The presence of rabbits did result in intermediate vole densities in 1998, but had no effect in the following years. Minimum numbers alive and total captures (not shown) gave identical results. Overall, 4.1% of the recaptured voles were found in different blocks, whereas the exchange among grazing treatments was 23.6% between 'Rabbits + Voles' and the 'Voles only' treatment, and only 0.5% between the 'Cattle + Rabbits + Voles' treatment and the two other treatments combined. Most voles (71.8%) were thus recaptured within the same block and grazing treatment where they had been caught first.

Vole weight did not differ significantly among treatments within years, nor among years for individual treatments (see Appendix A: Table 1).

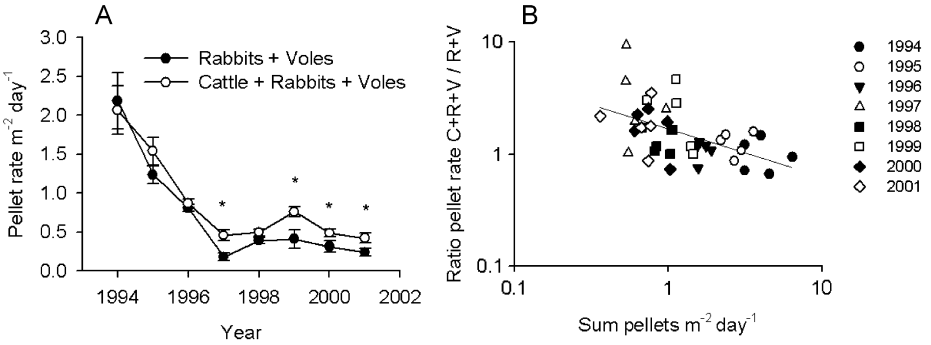

Fig. 2. Rabbit pellet rates (A) over the course of the experiment in the presence and absence of cattle grazing. Significantly different pellet rates ($P < 0.05$) are indicated by an asterisk (*). (B) Amount of pellets found in the treatment with Cattle + Rabbits + Voles (C + R + V) relative to the treatment without cattle (Rabbits + Voles, R + V) plotted against the total amount of pellets found in both treatments (sum pellets). $R^2 = 0.28$, $P < 0.001$.

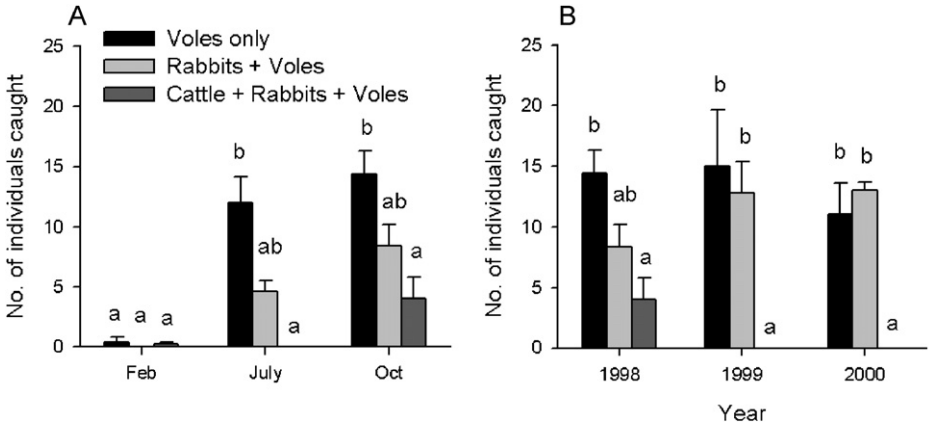

Fig. 3. Vole numbers under different grazing treatments: minimum number of individuals in three periods during the year 1998 (A) and minimum number of individuals in October of 1998, 1999 and 2000 (B). Data represent means ± S.E. Different letters indicate statistically significant differences in number of voles caught among the grazing treatments within each year or season ($P<0.05$).

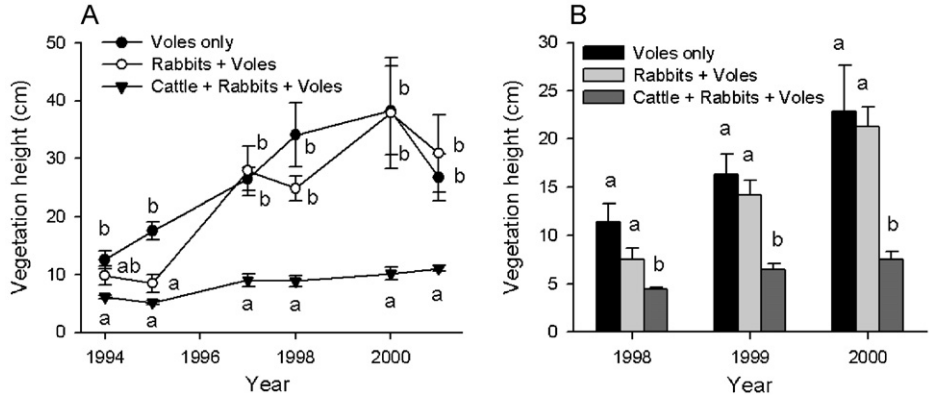

Fig. 4. Vegetation height (cm) at peak standing crop in the grazing treatments during the experiment (A); in October, during vole catches (B). Data represent means ± S.E. Different letters indicate statistically significant differences in vegetation heights among grazing treatments within each year ($P<0.05$).

Vegetation height

Cattle grazing significantly reduced vegetation height at peak standing crop compared to the exclosure treatments (Fig. 4A, log-transformation: $F_{2,12} = 27.63$, $P<0.001$). Vegetation height in the exclosures increased over the course of the experiment ($F_{5,60} = 45.73$, $P<0.001$). While there was a significant interaction between grazing treatment and year on vegetation height ($F_{10,60} = 4.02$, $P<0.001$), the effect of grazing treatment was significant within each year (Fig. 4A). The difference in vegetation height persisted through October (Fig. 4B), although vegetation had decreased in the exclosures compared to peak vegetation height (Fig. 4A). In October, vegetation height was significantly lower in the cattle grazed treatment ($F_{2,12} = 30.42$, $P<0.001$), compared to both exclosure treatments. There was no significant interaction between grazing treatment and year ($F_{4,24} = 1.56$, $P = 0.22$). Overall, the vegetation was significantly higher in the year 2000 compared to the other years ($F_{2,24} = 13.16$, $P<0.001$). The number of voles was positively related to vegetation height (Pearson correlation $r = 0.50$, $P = 0.001$, $n = 45$), whereas rabbit pellet rate was negatively related to vegetation height ($r = -0.57$, $P = 0.001$, $n = 30$); data from 1998 to 2000 combined.

Food quantity and quality

Standing crop of the vegetation changed strongly over the seasons, but was similar across grazing treatments (see Appendix A: Table 2), with the vegetation in all plots strongly dominated by grasses. Flower stem density was also mostly affected by the season, but not by the grazing treatments (see Appendix A: Table 2).

Nitrogen concentration in the plants depended on time of year ($F_{2,64} = 15.0$, $P<0.001$), the plant species sampled ($F_{2,32} = 66.6$, $P<0.001$) and the grazing treatment ($F_{2,32} = 70.2$, $P = 0.026$). There were also significant interactions between the season and species sampled ($F_{4,64} = 14.6$, $P<0.001$), as well as season and

grazing treatment (see Appendix A: Table 3, $F_{4,64} = 5.9$, $P < 0.001$). Post-hoc Tukey tests showed that vegetation N concentration was highest in green leaves of *Holcus*, then in green leaves of *Festuca* and then in the separately randomly collected living grass biomass samples, which consisted of multiple grass species. Plant N concentration was not significantly different among grazing treatments, with the exception of *Holcus* in May, which contained the lowest N concentration in the 'Cattle + Rabbits + Voles' treatment and the highest in the 'Rabbits + Voles' treatment with the 'Voles only' treatment being intermediate (see Appendix A: Table 3).

Rabbit and vole diet

The vegetation was dominated by six plant species, which collectively made up more than 80% of total plant cover in all grazing treatments (Fig. 5A). The lawn-forming grasses *A. capillaris* and *F. rubra* declined, whereas the tall grass *H. lanatus* and the sedge *Carex hirta* increased in abundance where cattle and subsequently rabbits were excluded (Fig. 5A). However, only the cover of *Holcus* was significantly different among the grazing treatments (Kruskall–Wallis test: $H_2 = 7.22$, $P = 0.027$; for the five other species $P > 0.05$). The abundance of *Holcus* was significantly different between the treatment with 'Cattle + Rabbits + Voles' and 'Voles only', whereas the *Holcus* cover in the treatment with 'Rabbits + Voles' was intermediate (Fig. 5A). Comparing diet choice and vegetation composition in July revealed that rabbits and voles behaved as generalist herbivores with diet choice reflecting the vegetation composition on offer (Figs. 5A and B). For rabbits, diet choice correlated best with vegetation composition in the 'Cattle + Rabbits + Voles' treatment ($r = 0.95$, $P < 0.001$, $n = 48$ plant species), followed by 'Rabbits + Voles' ($r = 0.92$, $P < 0.001$). Vole diet correlated best with the vegetation composition of the 'Rabbits + Voles' treatment ($r = 0.90$, $P < 0.001$) followed by the 'Cattle + Rabbits + Voles' treatment ($r = 0.82$, $P < 0.001$) and least with the 'Voles only' treatment ($r = 0.69$, $P < 0.001$).

Rabbit and vole diet through the year was rather similar (see Appendix A: Figs. 6A and B). Both rabbits and voles ate a lot of seeds when these were available, notably in June and July. The rest of the year they were more folivorous.

Discussion

We have shown that two species of small herbivores, European rabbits and common voles, responded differently to cattle grazing. Rabbits preferred the vegetation grazed by cattle, whereas voles preferred the vegetation where cattle were excluded.

Generally, responses of small rodent abundance to ungulate grazing have been shown to be negative in multiple combinations of ungulate and rodent species: red deer (*Cervus elaphus*) and wood mice (*Apodemus sylvestris*) in Dutch deciduous forest (Smit et al., 2001), sheep and field voles (*Microtus agrestis*) at a Norwegian alpine meadow (Steen et al., 2005), sheep, cattle and field voles at two Danish wet meadows (Schmidt et al., 2005), sheep, cattle and field voles at Scottish upland meadows (Evans et al., 2006), cattle and multiple rodent species at the American short grass steppe (Milchunas, Lauenroth, & Burke, 1998), and multiple ungulates versus multiple rodent species at a Kenyan savanna (Keesing, 1998). This seems, therefore, to be a universal response, although the underlying mechanisms have been shown to vary. The negative effects can be caused

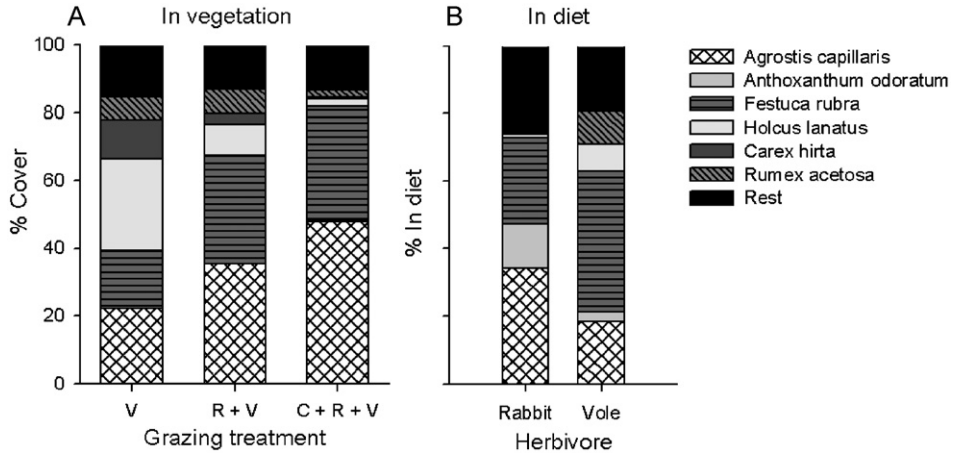

Fig. 5. Vegetation composition of the grazing treatments (A) in July 2001 representing the most abundant plant species, four grasses, one sedge (*Carex hirta*) and one herb (*Rumex acetosa*) and other species pooled together as Rest. (B) Rabbit and vole diet in July 2001. Grazing treatments are indicated as V, Voles only, R + V, Rabbits + Voles and C + R + V, Cattle + Rabbits + Voles.

by food competition (reduced food availability or quality), or increased predation risk. In the Kenyan savanna (Keesing, 1998) and alpine meadow (Steen et al., 2005), the negative effect of ungulates on rodent abundance is attributed to food competition. Ungulates had no effect on vegetation structure in the savanna and only a very small effect on plant cover in the alpine meadows. In the wet meadows (Schmidt et al., 2005), deciduous forest (Smit et al., 2001) and in our study of the floodplain grassland, ungulate grazing has a strong effect on vegetation structure (height or cover), resulting in a negative trend in rodent abundance.

In our study, the observed negative impact of ungulate grazing on rodent habitat choice, was likely due to reduced cover from predators rather than to food competition. Vegetation height increased when cattle were excluded, but standing crop was generally not different among grazing treatments. Under cattle grazing, the vegetation was low, but very dense, whereas vegetation in the exclosures was high, but less dense (E. S. Bakker, unpublished data). Also, the nitrogen concentration in plants did not differ among grazing treatments. Vole diet corresponded most with the vegetation in the treatment grazed by 'Rabbits + Voles', but least with the treatment with 'Voles only', which contained the highest vole numbers. Therefore, diet choice does not seem to be the main factor influencing vole habitat preferences. Finally, vole weight did not differ among grazing treatments, which is consistent with the finding that food quantity and quality also did not differ significantly among grazing treatments (Keesing, 1998). Because we can exclude differences in food quality or quantity among the grazing treatments, the positive effect of excluding cattle grazing on common vole abundances is most likely due to increased vegetation height, resulting in reduced perceived predation risk. However, since we only measured food quantity and quality during 1 year, we cannot exclude that this may have played a role in the other years during our study.

For rabbits we find opposite results – rabbits preferred the vegetation where cattle grazed. Rabbits are shown to prefer nutritious vegetation (Bakker et al., 2005) as well as short vegetation (Iason, Manso, Sim, & Hartley, 2002). In our study, the grazed vegetation was not more nutritious and could thus not explain rabbit habitat preferences, at least not in the year in which we measured food quality. Rabbit diet corresponded most with the vegetation from cattle grazed plots; however, similarity with the vegetation where cattle were excluded was also very high. Thus, diet preferences may contribute to the observed rabbit preference for the vegetation grazed by cattle. Additionally, the low vegetation height under cattle grazing may have attracted rabbits. An experiment where vegetation height was manipulated, but nutritious value remained similar, showed that rabbits preferred the shortest vegetation, despite the fact that this did not result in the highest intake rates (Iason et al., 2002). While Iason et al. (2002) hypothesized that this preference for the shortest vegetation is due to increased outlook possibilities, as well as fast escape routes from predators, this has not been investigated. Of the few studies which have examined the interaction between ungulates and rabbit-sized herbivores, most have found facilitative interactions. European hares at the Dutch salt marsh of Schiermonnikoog were not affected by cattle grazing in the short term (5 years), but did prefer cattle grazed swards in the long term (30 years) due to the invasion of tall unpalatable species in the ungrazed treatment (Kuijper, Beek, van Wieren, & Bakker, 2007). Cattle and sheep grazing has been shown to facilitate herbivorous geese (Barnacle (*Branta leucopsis*) and Brent (*Branta bernicla*) geese) (Bos et al., 2005; Van der Graaf, Bos, Loonen, Engelmoer, & Drent, 2002), which has been attributed to increased abundance of food plants and reduced vegetation height under livestock grazing.

Cheng and Ritchie (2006) hypothesize that the facilitation effect may depend on habitat productivity. At low productivity, food availability is low and ungulates may act as competitors, despite a possible increase in food quality under ungulate grazing. In productive grasslands, food availability is sufficient and ungulates increase food quality, while also preventing the invasion of tall, unpalatable grasses, and improving visibility. This hypothesis is supported by several studies. At low vegetative production Utah prairie dogs suffered from simulated grazing (Cheng & Ritchie, 2006), whereas at the more productive mixed prairie a facilitation effect between bison and black-tailed prairie dogs has been observed (Krueger, 1986). Our study site has an intermediate to high plant production and we observe a facilitation effect between cattle and rabbits. The other examples of livestock facilitating geese and hares (Bos et al., 2005; Kuijper et al., 2007; Van der Graaf et al., 2002) come from salt marshes, which are highly productive systems (Olff et al., 1997).

It has generally been found that the relationship between ungulates and smaller herbivores is density dependent. In an unproductive short grass steppe, lagomorphs were facilitated at moderate cattle grazing intensity, but showed an equally strong decline at high grazing intensity (Milchunas et al., 1998). The density of livestock also influences the response of field voles; with stronger negative effects at higher densities of livestock (Evans et al., 2006; Schmidt et al., 2005; Steen et al., 2005). However, both in a wet meadow and an alpine meadow, field voles produced more fetuses and had a higher population growth rate, respectively, under intermediate livestock grazing intensity compared to no livestock grazing (Schmidt et al., 2005; Steen et al.,

2005). The authors hypothesized that this effect possibly resulted from a higher nutrient content of the vegetation in lightly grazed versus ungrazed meadows, but no data are available. Simulated high grazing intensity reduced prairie-dog growth rates significantly, whereas at lower grazing intensity, prairie dogs showed some preference for the grazed plots (Cheng & Ritchie, 2006). Large herbivore grazing thus seems to generally improve food quality at low grazing intensities; however, their positive effect may be reversed when too much vegetation is removed.

In this study, we demonstrate a relationship between rabbit density and the importance of facilitation – rabbit density declined over the study period, whereas the preference for the cattle grazed treatment increased. This could point to an increase of the importance of facilitation at declining rabbit densities. However, since the decline in rabbits coincided with the aging of our exclosures, it is difficult to say whether this is a causal relationship.

We conclude that in productive grasslands, grazing by large herbivores reduces the abundance of small rodents whereas rabbits and probably other similar sized herbivores are facilitated. Using livestock in nature management to conserve biodiversity may thus have differential effects on small herbivore species.

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Appendix A. Supplementary Materials

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.baae.2007.10.009.

References

Arsenault, R., & Owen-Smith, N. (2002). Facilitation versus competition in grazing herbivore assemblages. *Oikos*, *97*, 313–318.

Bakker, E. S., Reiffers, R. C., Olff, H., & Gleichman, J. M. (2005). Experimental manipulation of predation risk and food quality: Effect on grazing behaviour in a central-place foraging herbivore. *Oecologia*, *146*, 157–167.

Bell, R. H. V. (1971). A grazing ecosystem in the Serengeti. *Scientific American*, *225*, 86–93.

Belovsky, G. E. (1997). Optimal foraging and community structure: The allometry of herbivore food selection and competition. *Evolutionary Ecology*, *11*, 641–672.

Bokdam, J. (1987). Foerageergedrag van jongvee in het Junner Koeland in relatie tot het voedselaanbod. In S. De Bie, W. Joenje, & S. E. Van Wieren (Eds.), *Begrazing in de natuur* (pp. 165–186). Pudoc.

Bos, D., Loonen, M. J. J. E., Stock, M., Hofeditz, F., Van der Graaf, A. J., & Bakker, J. P. (2005). Utilisation of Wadden Sea salt marshes by geese in relation to livestock grazing. *Journal for Nature Conservation*, *13*, 1–15.

Cheng, E., & Ritchie, M. E. (2006). Impacts of simulated livestock grazing on Utah prairie dogs (*Cynomys parvidens*) in a low productivity ecosystem. *Oecologia*, *147*, 546–555.

Cid, M. S., & Brizuela, M. A. (1990). Grass blade and sheath quantification by microhistological analysis. *Journal of Wildlife Management*, *54*, 349–352.

Demment, M. W., & Van Soest, P. J. (1985). A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *American Naturalist*, *125*, 641–672.

Du Toit, J. T., & Owen-Smith, N. (1988). Body size, population metabolism, and habitat specialization among large African herbivores. *American Naturalist*, *133*, 736–740.

Evans, D. M., Redpath, S. M., Elston, D. A., Evans, S. A., Mitchell, R. J., & Dennis, P. (2006). To graze or not to graze? Sheep, voles, forestry and nature conservation in the British uplands. *Journal of Applied Ecology*, *43*, 499–505.

Hofmann, R. R. (1989). Evolutionary steps of ecophysiological adaptation and diversification of ruminants: A comparative view of their digestive system. *Oecologia*, *78*, 443–457.

Huisman, J., & Olff, H. (1998). Competition and facilitation in multispecies plant–herbivore systems of productive environments. *Ecology Letters*, *1*, 25–29.

Iason, G. R., Manso, T., Sim, D. A., & Hartley, F. G. (2002). The functional response does not predict the local distribution of European Rabbits (*Oryctolagus cuniculus*) on grass swards: Experimental evidence. *Functional Ecology*, *16*, 394–402.

Illius, A. W., & Gordon, I. J. (1992). Modelling the nutritional ecology of ungulate herbivores: Evolution of body size and competitive interactions. *Oecologia*, *89*, 428–434.

Jacob, J., & Brown, J. S. (2000). Microhabitat use, giving-up densities and temporal activity as short- and long-term anti-predator behaviors in common voles. *Oikos*, *91*, 131–138.

Keesing, F. (1998). Impacts of ungulates on the demography and diversity of small mammals in central Kenya. *Oecologia*, *116*, 381–389.

Keesing, F. (2000). Cryptic consumers and the ecology of an African Savanna. *Bioscience*, *50*, 205–215.

Kotler, B. P., & Blaustein, L. (1995). Titrating food and safety in a heterogeneous environment: When are risky and safe patches of equal value? *Oikos*, *74*, 251–258.

Krueger, K. (1986). Feeding relationships among bison, pronghorn, and prairie dogs: An experimental analysis. *Ecology*, *67*, 760–770.

Kuijper, D. P. J., Beek, P., van Wieren, S. E., & Bakker, J. P. (2007). Time-scale effects in the interaction between a large and a small herbivore. *Basic and Applied Ecology* 〈doi: 10.1016/j.baae.2006.08.008〉, in press.

Londo, G. (1976). The decimal scale for relevés of permanent quadrats. *Vegetatio*, *33*, 61–64.

McNaughton, S. J. (1984). Grazing lawns: Animals in herds, plant form, and coevolution. *American Naturalist*, *124*, 863–886.

Milchunas, D. G., & Lauenroth, W. K. (1993). Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs*, *63*, 327–366.

Milchunas, D. G., Lauenroth, W. K., & Burke, I. C. (1998). Livestock grazing: Animal and plant biodiversity of shortgrass steppe and the relationship to ecosystem function. *Oikos*, *83*, 65–74.

Olff, H., De Leeuw, J., Bakker, J. P., Platerink, R. J., Van Wijnen, H. J., & De Munck, W. (1997). Vegetation succession and herbivory in a salt marsh: Changes induced by sea level rise and silt deposition along an elevational gradient. *Journal of Ecology*, *85*, 799–814.

Olff, H., & Ritchie, M. E. (1998). Effects of herbivores on grassland plant diversity. *Trends in Ecology and Evolution*, *13*, 261–265.

Olff, H., Ritchie, M. E., & Prins, H. H. T. (2002). Global environmental controls of diversity in large herbivores. *Nature*, *415*, 901–904.

Prins, H. H. T., & Olff, H. (1998). Species-richness of African grazer assemblages: Towards a functional explanation. In: D. M. Newbery, H. H. T. Prins, N. D. Brown (Eds.), *Dynamics of tropical communities* (pp. 449–490). BES.

Schmidt, N. M., Olsen, H., Bildsoe, M., Sluydts, V., & Leirs, H. (2005). Effects of grazing intensity on small mammal population ecology in wet meadows. *Basic and Applied Ecology*, *6*, 57–66.

Seber, G. A., & Pemberton, J. R. (1979). The line intercept method for studying plant cuticles from rumen and fecal samples. *Journal of Wildlife Management*, *43*, 916–925.

Sierra, P. V., Cid, M. S., Brizuela, M. A., & Ferri, C. M. (2005). Microhistological estimation of grass leaf blade percentages in pastures and diets. *Rangeland Ecology & Management*, *58*, 207–214.

Smit, R., Bokdam, J., Den Ouden, J., Olff, H., Schot-Opschoor, H., & Schrijvers, M. (2001). Effects of introduction and exclusion of large herbivores on small rodent communities. *Plant Ecology*, *155*, 119–127.

StatsSoft Inc. (2005). *Statistica 7.1*. Tulsa, USA.

Steen, H., Mysterud, A., & Austrheim, G. (2005). Sheep grazing and rodent populations: Evidence of negative interactions from a landscape scale experiment. *Oecologia*, *143*, 357–364.

Stewart, D. R. M. (1967). Analysis of plant epidermis in faeces: A technique for studying the food preferences of grazing herbivores. *Journal of Applied Ecology*, *4*, 83–111.

Stewart, K. E. J., Bourn, N. A. D., & Thomas, J. A. (2001). An evaluation of three quick methods commonly used to assess sward height in ecology. *Journal of Applied Ecology*, *38*, 1148–1154.

Van der Graaf, A. J., Bos, D., Loonen, M. J. J. E., Engelmoer, M., & Drent, R. H. (2002). Short-term and long-term facilitation of goose grazing by livestock. *Journal of Coastal Conservation*, *8*, 179–188.

Van der Meijden, R. (1990). *Heukels' Flora van Nederland*. Wolters-Noordhoff.

Vavra, M., & Holechek, J. L. (1980). Factors influencing microhistological analysis of herbivore diets. *Journal of Range Management*, *33*, 371–374.

Wilmshurst, J. F., Fryxell, J. M., & Bergman, C. M. (2000). The allometry of patch selection in ruminants. *Proceedings of the Royal Society London B*, *267*, 345–349.

Ydenberg, R. C., & Prins, H. H. T. (1981). Spring grazing and the manipulation of food quality by barnacle geese. *Journal of Applied Ecology*, *18*, 443–453.